ARTHROPOD PATTERN THEORY: A NEW APPROACH TO ARTHROPOD PHYLOGENY

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A review of fossil, morphologic, developmental, and genetic evidence suggests a series of new and novel hypotheses to explain the evolution of arthropods. Termed Arthropod Pattern Theory (APT), these hypotheses are: 1. That the biramous limb was formed by the basal fusion of uniramous limbs; 2. That a uniramian diplosegment (or paired monosegments) is homologous to a single body segment, or duplomere, of arthropods bearing biramous limbs; 3. That suites of segments evolve as units with tagmata transitions, location of gonopores and anus, and body terminations occurring at specific points along the body that are shared among disparate groups. APT requires a complete reassessment of old assumptions about segment homologies within articulates. ☐ *Arthropoda, Crustacea, Remipedia, Euthycarcinoidea, Drosophila genetics, segment pairing, uniramy, biramy, phylogeny.*

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Seldom does the study of fossils cause a complete reassessment of previous assumptions about evolution within an entire phylum. However, the problematic arthropod, *Tesnusocaris goldichi* (Brooks, 1955), from the Late Mississippian of west Texas (Schram and Emerson, 1986; Emerson and Schram, in press) and other fossils reveal some previously unsuspected features of arthropod anatomy that necessitate such a re-evaluation.

Brooks was uncertain in his original description of *T. goldichi* as to the exact affinities of this species, and he compared this fossil with crustaceans such as branchiopods and cephalocarids. Hessler (1969) rejected the latter assignment, and Schram (1983, 1986) suggested possible affinities with the Class Remipedia. The new material reveals the cephalic anatomy of a remipede, but thoracic appendages with most peculiar features (Fig. 1). Each trunk segment of *Tesnusocaris* possesses two pairs of ventrally placed uniramous limbs: a medial pair directed posteriorly and possibly used in sculling, and a ventral pair directed laterally and apparently used in rowing (Emerson and Schram, in press). The significance of these limbs, became apparent when they were compared to other peculiar late Palaeozoic arthropods (Emerson and Schram, 1990). This comparison suggested a novel hypothesis for the evolution of the biramous crustacean limb, *viz.*, that biramy evolved by means of the fusion of basal podomeres of adjacent uniramous limbs.

We found the above anatomical observations and the concepts they suggested interesting, although the stratigraphic position of *Tesnusocaris* in the Carboniferous might seem to contradict interpretation of this fossil as an ancestral crustacean. However, we are not proposing that *Tesnusocaris* is an ancestor, merely that its trunk limb anatomy represents a more primitive condition than that seen in biramous arthropods. Furthermore, its stratigraphic position is unimportant because there appear to be even earlier remipedes in the fossil record (Mikulic *et al.*, 1985, fig. 16). Certainly, one caveat of paleontology is that 'things are always older than you think they are', e.g. discoveries of the earliest uniramians (Mikulic *et al.*, 1985; Robison, 1990).

Other kinds of arthropods seem to share this distinctive arrangement of trunk limbs, but previously they were not recognised as such because no one had realised the possibility of such an anatomical condition. One of the best candidates is the Cambrian Burgess Shale arthropod *Branchiocaris pretiosa*. Briggs (1976) reconstructed flap-like limbs attached to a ventrolateral ridge on the trunk (Fig. 2B). He noted proximal elements that appeared to extend along the medial

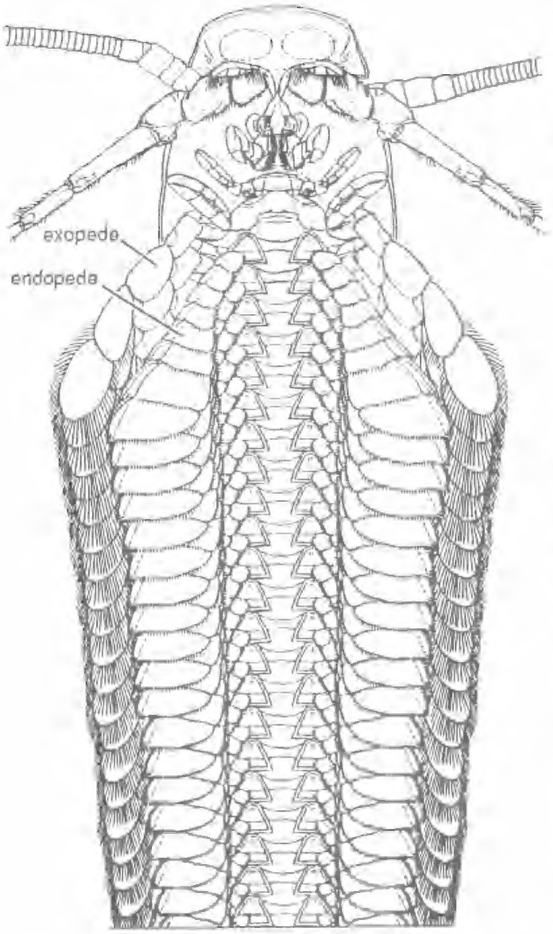

FIG. 1. Ventral reconstruction of *Tesnusocaris goldichi* from the Upper Mississippian of Texas (from Emerson and Schram, in press).

edge of the flap toward the body midline. Briggs designated the proximal elements as reinforcing structures or endites along the flaps, but in the text admitted difficulties in interpreting the fossils and pointed out the tentative nature of his reconstruction of the limbs. However, published camera lucida drawings (Fig. 2A) reveal that these medial elements have a more sagittal position than the lateral flaps. This arrangement, with rami of at least seven podomeres, simple transverse articulations between podomeres, and a flipper-like outline, suggests to us that the sagittal elements bear a clear resemblance to those of *Tesnusocaris*. The flap-like lateral elements on *Branchiocaris*, therefore, are comparable to the ventrolateral pair of limbs of *Tesnusocaris*. Careful examination of other fossil arthropods may reveal additional examples of this arrangement of trunk limbs.

The peculiar form and position of the limbs in relation to the trunk segments of animals like *Tesnusocaris* require a new set of terms to describe appendages and segments in arthropods (Emerson and Schram, 1990). The segments of insects and some myriapods are *monomeres* (or *monosegments*) with each segment bearing one pair of uniramous limbs. The monomeres of many myriapods and the fossil euthycarcinoideans are paired with the dorsal tergites fused and the ventral sternites free, thus forming *diplomeres* (or *diplosegments*). Each diplomere bears two sets of uniramous limbs, one set on each sternite. We contend that crustaceans, and by extension other arthropods that bear biramous limbs, have completely fused the ventral sternites of adjacent segment pairs, as well as the dorsal tergites, to form *duplomeres*. Arthropods like *Tesnusocaris* and possibly *Branchiocaris* are therefore *duplopodous*, displaying two sets of uniramous limbs on each *duplosegment*. The medial pair of trunk limbs on *Tesnusocaris* are known as the *endopedes*, the lateral set are the *exopedes*. Except for the above, most other fossil and living arthropods are biramous, with a single set of branched limbs on each duplosegment, although secondarily uniramous limbs have reoccurred several times.

The Euthycarcinoidea were apparently aquatic creatures that lived from Carboniferous to Triassic time. The most recent review of the group (Schram and Rolfe, 1982) agreed with the suggestion of Bergström (1980) that placed the problematic euthycarcinoideans within the Uniramia. The trunk of these fossils is divided into an anterior limb-bearing region and a posterior limbless area; differences in this regard are the basis for two subgroups (Schram and Rolfe, 1982; Starobogatov, 1988): the Sottyxerxidae (= Sottyxerxiformes) have a long anterior trunk (Fig. 3A), and the Euthycarcinidae (= Euthycarciniformes) possess a short anterior region (Fig. 3B). In both groups, the trunk is characterised by a series of diplo- and triplosegments bearing uniramous limbs that are evocative of similar conditions in extant myriapods. The euthycarcinoidean head is not well known, but appears to resemble the hypothetical primitive arthropod head of Snodgrass (1952), with an anterior procephalon bearing a single pair of antennae and a distinct posterior gnathocephalon bear-

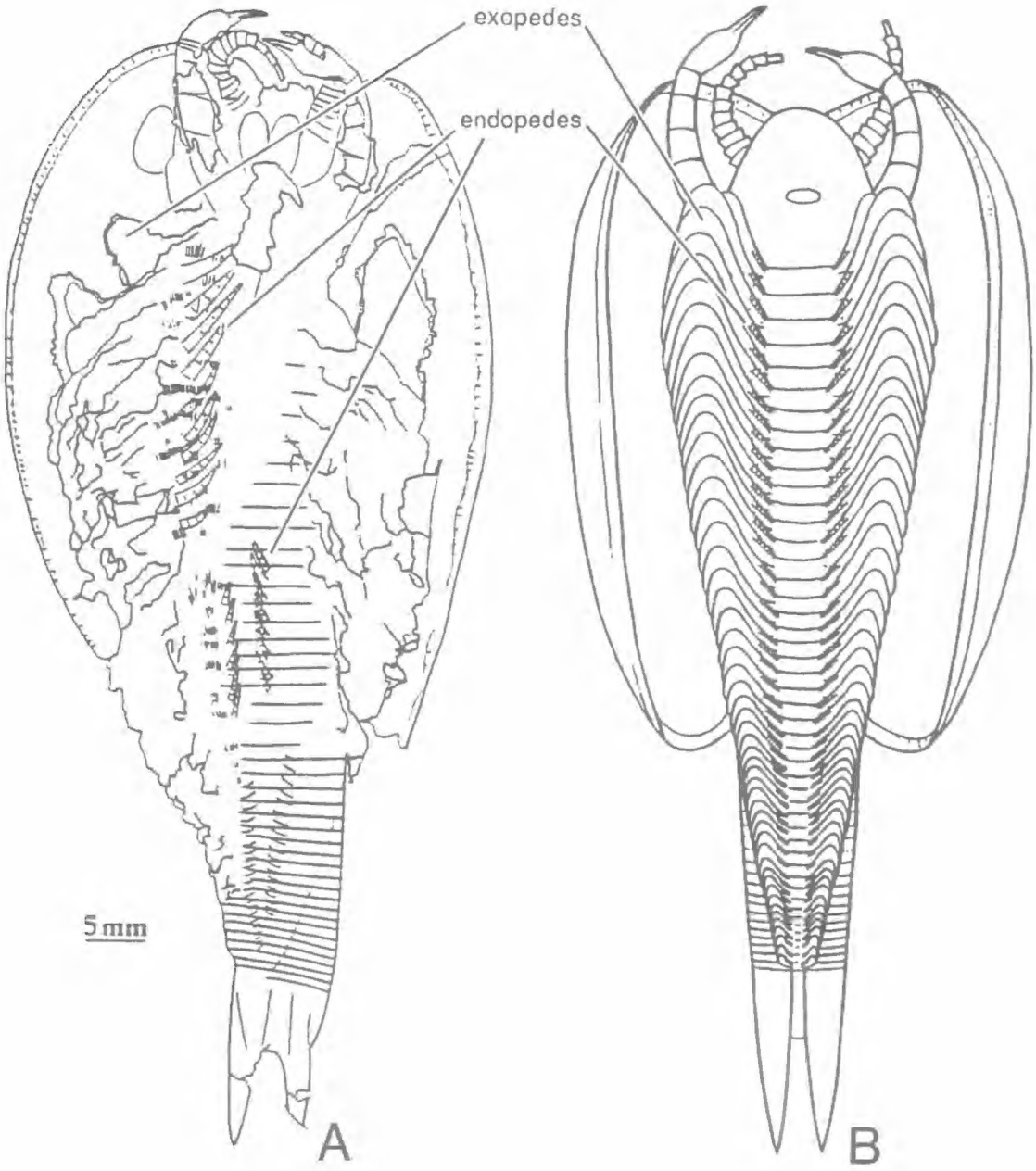

FIG. 2. Our interpretation of *Branchiocaris pretiosa*, from the Cambrian of British Columbia. A, Camera lucida drawing of USNMP 189028. B, Ventral reconstruction of the adult (modified from Briggs, 1976).

ing the mouth and a set of rarely preserved mandibles.

Comparison of *Tesnusocaris*, possibly *Branchiocaris*, and the euthycarcinoideans with the uniramians and crustaceans suggested to Emerson and Schram (1990) a new interpretation of arthropod limb evolution. However, so unusual is this interpretation that the fossils are insufficient to justify it; confirmation comes from the fields of comparative anatomy, ontogeny, and developmental genetics. The elements of Arthropod Pattern Theory (APT) are considered below.

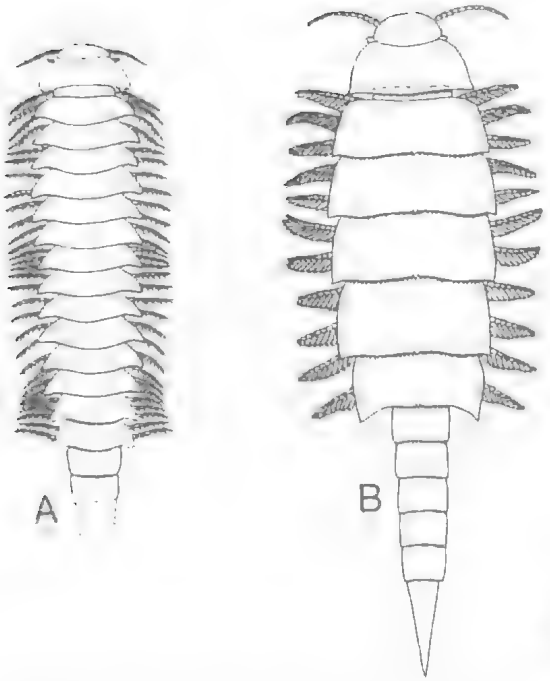

FIG. 3. Dorsal reconstruction of Euthycarcinoidea from the Middle Pennsylvanian of Illinois. A, *Pieckoxerxes pickoae*. B, *Kottixerxes gloriosus*. (modified from Schram and Rolfe, 1982).

HYPOTHESIS ONE

The biramous limb of Crustacea (and probably all arthropods bearing such) evolved by means of the basal fusion of duplopodous, uniramous limbs.

In analysing *Tesnusocaris*, Emerson and Schram (in press) considered the possibility that the two sets of separate uniramous limbs on single trunk segments were only apparently so, i.e. that the arrangement of structures seen in the fossils might represent biramous limbs in which the protopods were incorporated, or fused, into the body wall. This would be analogous to a situation in isopods. This alternative was rejected on both structural and functional grounds. The exopedes and endopedes appear to have functioned in distinctly different ways from each other and thus likely possessed different musculatures; their physical separation on the *Tesnusocaris* trunk somites seems too great to have been derived from a single limb pair; the basal segments of both limbs resemble true coxae; and the number of podomeres is more (not less) than would be expected if a biramous limb fused proximal articles into a body wall.

We concluded (Emerson and Schram, in press) that the trunk limb anatomy of *Tesnusocaris* represents two separate sets of appendages on each trunk segment. Furthermore, distinct limb and segment morphologies are recognized among living and fossil groups (Fig. 4). One condition occurs when the tergites of adjacent somites fuse to form diplosegments, while the still separate sternites each bear a pair of uniramous limbs. Examples of this condition are noted in diplopodous myriapods and euthycarcinoideans (Fig. 4A). A second condition occurs in which each monosegment bears a single pair of uniramous limbs. Examples of this condition are seen in geophilomorph centipedes (Fig. 4B) and insect thoraxes. A third condition exists

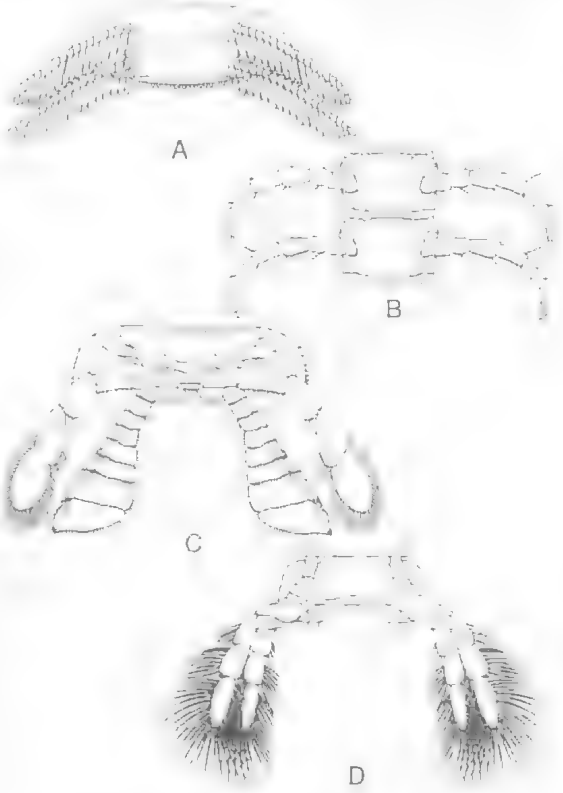

FIG. 4. Ventral views of trunk somites of various arthropods. A, Diplosegment of a generalized euthycarcinoidean with each sternite bearing a pair of uniramous limbs. B, Two monosegments of a geophilomorph centipede with uniramous limbs. C, Duplosegment of *Tesnusocaris goldichi* with two sets of uniramous limbs. D, Duplosegment of a generalized nectiopodan remipede with biramous limbs (from Emerson and Schram, 1990).

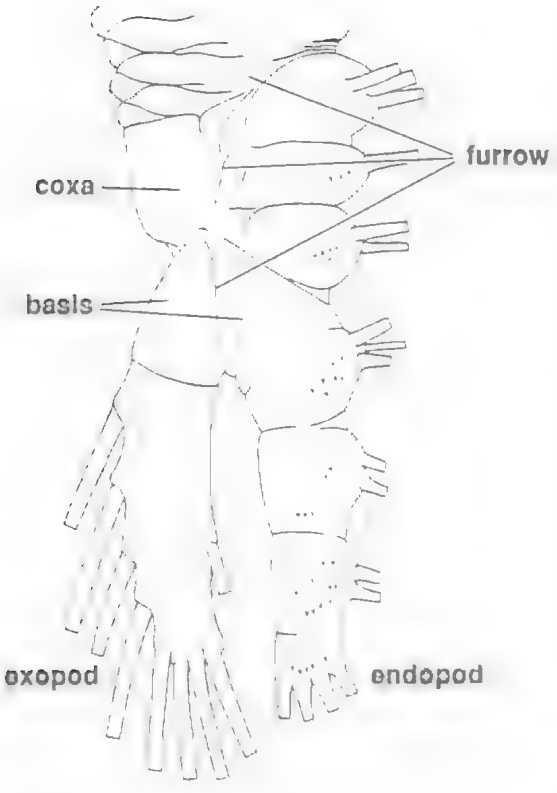

FIG. 5. Maxillule of *Skara anulata* displaying the median furrow on the protopod (from Müller and Walossek, 1985).

when both tergal and sternal fusion occur to form, what we call, duplosegments. Separate pairs of uniramous appendages give the appearance of two sets of limbs on each duplosegment. The prime example of this is *Tesnusocaris* (Fig. 4C). We hypothesise that in the final condition the basal podomeres of the separate limb pairs of a duplosegment fuse to form the common protopod of a biramous limb with exopod and endopod branches (Fig. 4D). This is exemplified by crustaceans that bear biramous limbs, trilobites, and many of the Burgess Shale arthropods.

The above may seem startling. Nevertheless, the hypothesis that there was a tendency in the early evolution of crustaceans to fuse basal podomeres gains some support from the study of several fossil and living arthropods.

For example, an interesting, but problematic, condition occurs on certain fossils. Distinct furrows exist (Fig. 5) on the anterior and posterior faces of the coxae and bases in many of the Cambrian Örsten crustaceans from Sweden (Müller and Walossek, 1985, 1988). [Lauterbach (1988) questions whether these fossils are really crustaceans.] Although the interpretation of these furrows is open to speculation, and issues of fossil preservation should not be overlooked, in light of our hypothesis, these furrows could be indications of the remnant of fused medial and lateral elements in the formation of the protopod in animals such as *Skara* and *Bredocaris*.

A more compelling line of support comes from observations of Ito (1989) who, in comparing the morphology of the copepodan trunk limb to that of nectiopodan remipedes, concluded that the basal podomeres of the nectiopodan exopod and endopod fused to each other to form the basis of the copepodan protopod (Fig. 6). Ito felt that this fusion was supported by the arrangement of the intrinsic muscles of the appendages of the two groups in question, and by the positional homology of the setose accessory fold found at the base of the exopod in many nectiopodans with the setose lateral arm of the basis in copepods. If a process of segment fusion could have evolved the crustacean basis, then it is possible that an identical process could have produced the coxa.

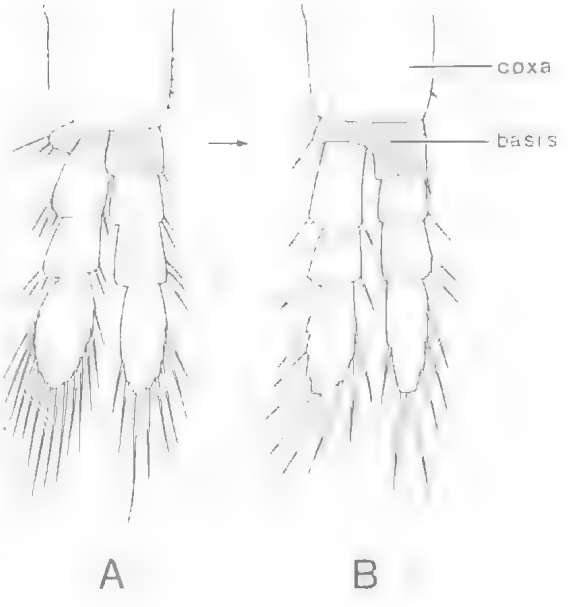

FIG. 6. Trunk limbs. A, nectiopodan; B, copepod. Shaded portion designates postulated homologous regions of the proximal podomeres of nectiopodan rami and the copepod basis (from Ito, 1989)

Although the data above suggest only that the crustacean biramous limb could have been formed by the fusion of duplopodous limbs, this process may also be extended to an explanation of the biramous limbs of other schizoramians such as trilobites, various Cambrian Burgess Shale arthropods, and extant and extinct cheliceriforms. Briggs and Fortey (1989) presented a cladistic analysis of the Burgess Shale and other arthropods that suggests that cheliceriforms, trilobites, and their Cambrian allies are more derived schizoramians than are crustaceans. We believe that in general their conclusion is valid, but just how the specific interrelationships may sort themselves according to APT features awaits more detailed development of our own character matrix.

HYPOTHESIS TWO

A uniramian diplosegment, or two monomeres, is homologous to a single crustacean (and, by extension, other biramian arthropods) body segment, or duplosegment.

The fundamental axiom of comparative anatomy of articulate invertebrates (arthropods and their allies) has been that all body segments among phyla within this group are homologous. Without any evidence to the contrary, it has never been thought necessary to question this assumption. However, if the origin of the biramous limb is hypothesised to derive from the fusion of duplopodous, uniramous elements, then that basic assumption must now be questioned. We sought support from comparative anatomy.

The nervous system of crustaceans provides several excellent examples in this regard. In the central nervous system of the cephalocarids (Elofsson and Hessler, 1990) as well as branchiopods, such as notostracans, anostracans, and conchostracans (Fig. 7C), the paired ventral cords are linked by two commissures in each segment of the head and trunk. Nerve cords in other adult crustaceans and arthropods typically exhibit various degrees of fusion, thus perhaps obscuring a similar pattern. However, in the annelids and uniramians such as centipedes, a single commissure or ganglion exists for each monosegment (Fig. 7A), and in diplopods there is only one fused ganglion per monosegment sternite, i.e. two per diplosegment (Fig. 7B). Where onychophorans fit in this regard is unclear, since they have multiple commissures along the entire length of the nerve cords but no well-organized ganglia that would mark the segments (Meglitsch and Schram, 1991: 354).

In the ontogeny of peracarid and stomatopod crustaceans, there are several instances of the occurrence of double ganglia in segments (Fig. 7D). Transitory anlagen of a second pair of ganglia occur in the sixth abdominal segments of mysids (Manton ,1928), some stomatopods (Shiino, 1942), tanaids (Scholl, 1963), and isopods (Strömberg, 1967). In addition, a transitory furrow occurs in the course of development on the sixth abdominal ganglia of amphipods (Weygoldt, 1958). The traditional interpretation of these phenomena has been that they represent the fleeting appearance of the ganglia of the supposedly ancestral seventh abdominal segment. Although this interpretation could be true, we feel that it is equally likely that these extra ganglia and the furrow may represent the delayed fusion of the second set of ganglia associated with the sixth abdominal duplomere.

A similar explanation could be applied to the strange, double arterial supply from the heart to the musculature of the first abdominal segment in certain stomatopods (Komai and Tung, 1931; Siewing, 1956; Schram, 1969). These arteries may not be a remnant of an extra segment in the anterior part of the stomatopod abdomen, as has been suggested, but rather may represent remnants within the circulatory system of a first abdominal duplosegment.

Reaka (1975, 1979) noted an unusual pattern of moult sutures in stomatopods. The median suture on the sixth, seventh, and anterior half of the eighth thoracomeres connects to a lateral suture on the posterior half of the eighth thoracic and the abdominal segments. Rather than indicating, as has been suggested, evidence for an extra monosegment in the anterior abdomen/posterior thorax, the divergent sutures within the last thoracomere may mark the separate components of an eighth thoracic duplosegment.

Dohle and Scholtz (1988) studied the early differentiation of limbs in peracarids. Two distinct cell lines give rise to the anterior and posterior regions of the limbs of the post-oral segments. It is possible that this pattern represents a remnant of the duplosegmental ancestry of those limbs, although an alternative hypothesis has been put forth based on the concept of parasegment compartmentalisation derived from work on *Drosophila* ontogeny (Martinez-Arias and Lawrence, 1985).

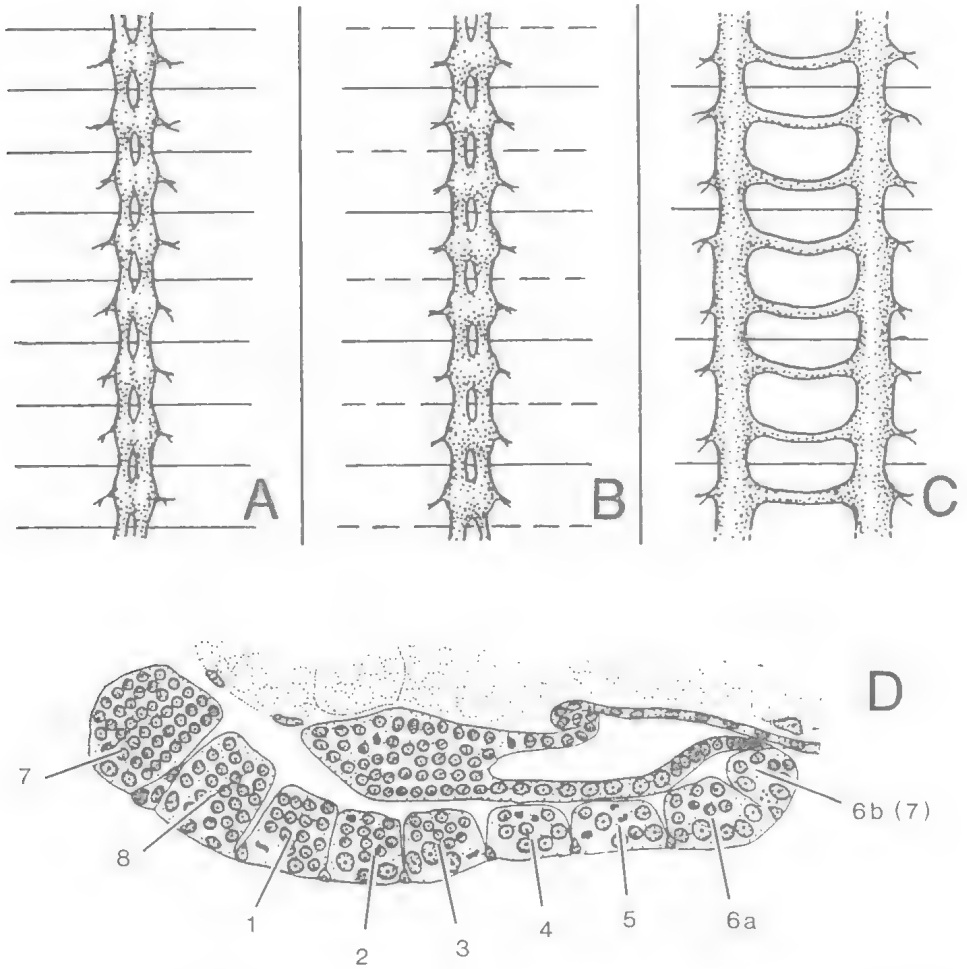

FIG. 7. Arthropod central nervous systems. A–C, Semi-diagrammatic representations of the paired ventral nerve cord of arthropods. A, Centipede, with one set of fused ganglia per monosegment; B, Diplopod, with one set of fused ganglia within each segmental component (dashed lines) of a diplosomite (solid lines); C, Conchostracan, widely spaced cords with two commissures within each duplosegment (from Emerson and Schram, 1990); D, Nerve ganglia development in *Heterotanais oerstedi* with last two thoracic and all abdominal anlagen numbered, the last two ganglia interpretable as either the last two of 7 abdominal monosegments (traditional view) or two portions of a 6th abdominal duplosegment (APT view) (from Scholl, 1963).

The above examples support our hypothesis that the crustacean segment is a composite, or duplosegment, formed from the fusion of two monosegments. Furthermore, ontogenetic and developmental patterns in uniramians seem to second the view that the segments of insects and myriapods are organized in a fundamentally different way than those of crustaceans.

In the ontogeny of *Drosophila*, the phenotypic expression of repeating monomeres (Fig. 8A) is governed by two types of pair-rule genes (Nüsslein-Volhard and Weischaus, 1980; Scott and O'Farrell, 1986), an odd pair-rule type that governs the expression of odd numbered segments, and an even pair-rule gene that controls the even numbered segments. The expression of individual monomeres depends on the interaction of both these loci. The discovery of this peculiar mode of segmental patterning was unexpected and startled those working on the genetics of fruit fly development (Nüsslein-Volhard and Weischaus, 1980: 287). This peculiar

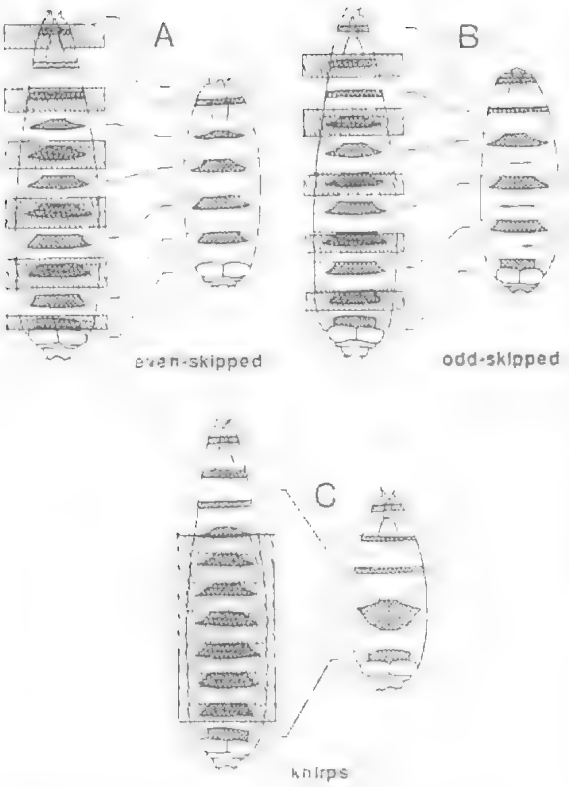

FIG. 8. Diagrammatic representations of gene mutants in *Drosophila* larvae. Pair-rule genes control expression of every other segment, be it odd or even. Gap genes control the expression of a series of segments (modified from Nüsslein-Volhard and Wieschaus, 1980).

control of segment development in *Drosophila* is still difficult to explain under the strictures of traditional views of articulate segmental homology. However, this genetic control is readily accountable in APT by the assumption of an arthropod synapomorphy of segmental patterning organized in units of two as seen in the comparative anatomy of fossil and living forms.

The manifestation of pair rules is evident in other extant uniramians as well. Scheffel (1965) noted that in the anamorphic centipedes two segments at a time are added with each moult stage, and Minelli and Bortolleto (1987) presented strong evidence for segmental pairing based on multiples of two in diplopods that typically add legs during anamorphic growth in units of two or powers thereof. Other epimorphic myriapods also exhibit some segment pairing in the trunk, *viz.* lithobiomorph and scutigeromorph centipedes, pauropods, and symphylans. In short, the segmental pairing seen throughout the uniramians, either in the genetics controlling development or the patterns of anamorphic growth and adult morphology, suggests that this feature was shared with their immediate ancestor.

In contrast to the segment pairing in uniramian ontogeny, biramian arthropods exhibit no such pattern. Segment budding in the germinal discs of crustacean embryos occurs only one at a time; and, while the appearance of segments in larvae displays no consistent pattern, leg buds in larvae typically appear one at a time (Schram, 1986). Itow (1985, 1986) found that segments appear one at a time during the early ontogeny of limulines. Although data are limited and circumstantial, budding of single segments in biramian arthropods instead of segment pairs is exactly what would be expected if a single biramian duplosegment is in fact homologous to two uniramian monosegments.

HYPOTHESIS THREE

Suites of segments in arthropods evolve as units, with the transition of tagmata, the location of gonopores and anus, and the body termination occurring at specific points along the body that are shared between disparate groups.

As we initially began our work, comparing nectiopodan remipedes, *Tesnusocaris*, and the two main groups of euthycarcinoideans, we noticed that certain zones along the length of the body seemed to be the focus of distinct anatomical events (Fig. 9). For example, duplomere 6 (d_6) not only marked the terminus of the head in the crustaceans, but also was the location of an anomalous monosegment in *Sottyxerxes multiplex* (not illustrated here) and was involved in some way in the appearance of triplosegments in the anterior trunks of all Euthycarcinidae. Furthermore, duplomeres 11–13 marked another region in these animals in which the female gonopore in nectiopodans, segmental anomalies in Sottyxerxidae, and postabdominal termination in Euthycarcinidae occurred. Finally, duplomeres 18–20 marked the location of the male nectiopodan gonopore as well as a transition of pre- and postabdominal tagmata in the sottyxerxids.

Initially, we viewed these co-occurrences as interesting but coincidental. If the patterning of

arthropod segmentation were under no particular control, we would have expected that the location of gonopores, tagmata transitions, and body terminations would have occurred randomly along the arthropod body. However, when we examined other arthropods, we noted that these same areas consistently marked either the location of prominent anatomical structures, or transitions of tagmata, or body terminations. We then realized that these patterns were not random at all.

We eventually came to refer to suites of segments as either 'fields' or 'nodes'. Fields are adjacent duplomeres that are for the most part regions of tagmatic stability, while nodes are suites of somites where anatomical events seem to focus (Figs 9–11). Duplomeres 1–4 (monomeres 1–8) mark the first field, duplomeres 5 and 6 (monomeres 9–12) are node one, duplomeres 7–10 are the second field, duplomeres 11–13 are node two, duplomeres 14–17 are the third field, duplomeres 18–20 are node three, and duplomeres 21 to the end of the body mark the fourth field. Thus the arthropod body can be divided into an alternating series of 4-2-4-3-4-3-n numbers of duplosegments (or 8-4-8-6-8-6-2n monosegments). In addition, secondary nodes appear to focus on duplomere 9 within the second field, in the euthycarcinid genera *Kottixerxes* and *Schramixerxes*, some maxillopodan crustaceans, and almost all cheliceriforms, and on duplomere 16 in many crustaceans.

As noted above, the nodes are the principle places where gonopores are located, tagma boundaries occur, and bodies terminate. When shifts in the location of these structures occur during the evolution of a group they appear to take place in quantum jumps from one node to the next. As with pair-rule genes in patterning of arthropod segment differentiations discussed above, another class of genes that has been studied in insect development, gap genes, seems relevant to understanding the control exerted over the patterning of arthropod body regions. Gap genes (Fig. 8B) govern the differentiation of suites of segments; and mutations in these genes result in the deletion of entire segment series. Consequently, it is now possible to visualize the apparent movement of anatomical structures forward in the arthropod body, such as gonopores and tagma boundaries, as gap mutations interact with regulatory genes to shorten the body and shift structures in quantum jumps within the framework of the underlying 4-2-4-3-4-3-n architectural plan of fields and nodes.

The Uniramia provide a clear example of pattern evolution (Table 1; Fig. 10). Among the centipedes, the longest bodied forms are the geophilomorphs with terminal gonopores. Other centipedes show anterior shifts of the gonopores and body terminus. Scolopendromorphs (Fig. 10) delete node three and the fourth field to shift their anus and terminal gonopores to the end of the third field, and scutigeromorphs and lithobiomorphs delete the third field with the result that the anus and terminal gonopore occur in the last segments of node two. In all centipedes, the beginning of the trunk occurs within node one. In the other myriapods, the gonopores open only on monomeres of node one while the anuses and body termini occur in the last monomeres of a more posterior field or node (Fig. 10). Colloboognathan diplopods bear gonopods and these are found on segments of node two. In the hexapod groups (insects and apterygotes) the thorax/abdomen transition is a node one event and gonopores are located at the end of the second field (Fig. 10). Thus, in uniramians, the location of gonopores and reproductive structures are located either in nodes or on the terminal segments of the fields just anterior to nodes. This pattern is so consistent that it allows us to predict, for example, that the gonopore of the strange fossil myriapod *Arthropleura* will be found probably in node one.

A similar, although more complex pattern can be found among the crustaceans (Table 2; Figs 9, 11). The longest bodied crustaceans with the most posterior location for gonopores are the nectiopodan remipedes (Fig. 9): the female pore is in node two, but the male pore is in node three. We predict that gonopores for the extinct *Tesnusocaris*, should they be found, will occur in either one or both of those same nodes. With some exceptions, gonopores of other crustaceans occur either in node two or node one. The exceptions are interesting in their own right in that their occurrence is not random. The Branchiura and Mystacocarida have gonopores on duplomere 9 (d_9) of the second field, while duplomere 16 (d_{16}) of the third field is the location of either gonopores or terminal anuses in several maxillopodan and phyllopodan groups. Both d_9 and d_{16} are two duplomeres forward of nodes two and three respectively. It is tempting to suggest, in light of what we know about gap mutations, that the shift forward in these animals might be due to a mutation that involved the expression in whole or in part of node one (a two duplomere node). The fact that these exceptions in the Crustacea are not

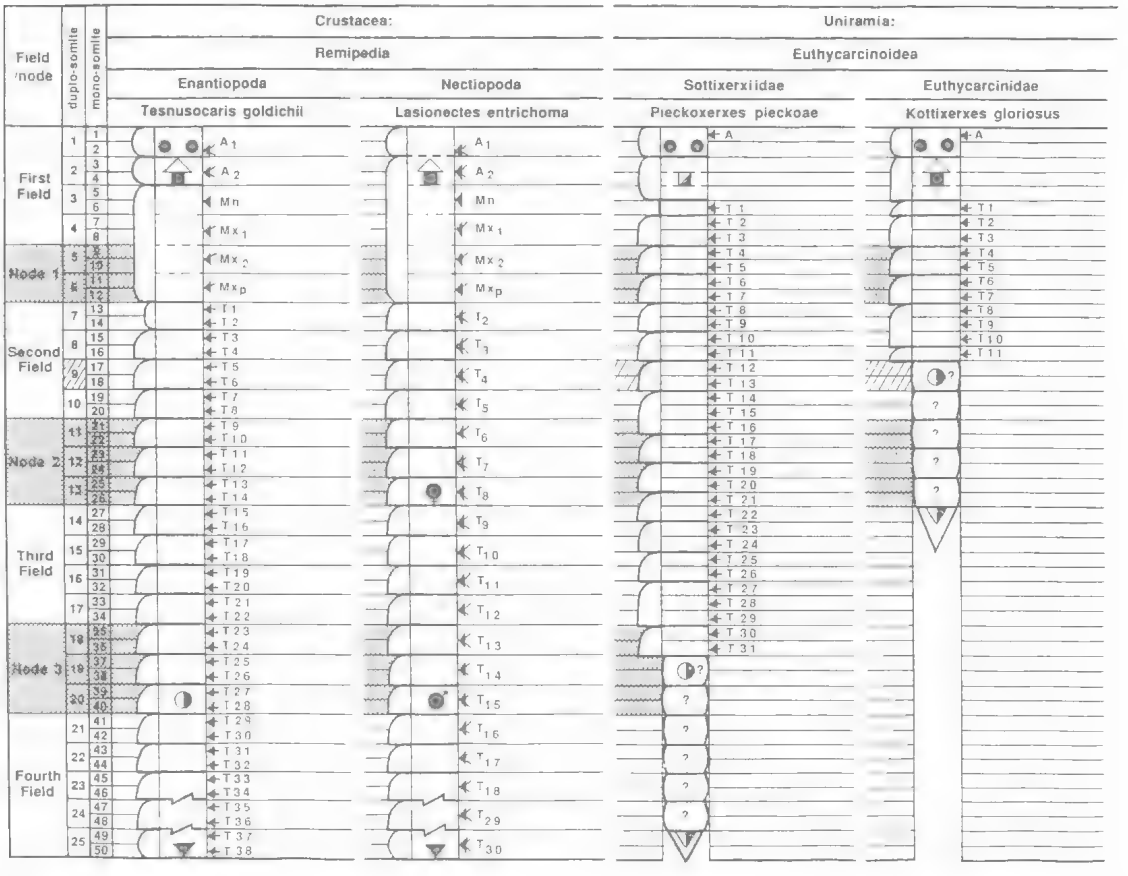

FIG. 9. Diagrammatic representations to illustrate some APT features of remipede crustacean and euthycarcinoidean uniramian body plans, with APT numeration to the left. The ? indicate uncertainty as to whether monomerous or diplomerous. Small circles = eyes, triangle = labrum, square = mouth, circle = gonopore, inverted triangle = anus, half shaded = predicted location.

random, but also conform to a pattern, indicates that some underlying genetic control of pattern formation is operational in the crustaceans.

Further confirmation of such field/node architecture is found in the patterns of early differentiation of the germinal disc of peracarids (Dohle and Scholtz, 1988). After the egg nauplius stage is passed through, the postnaupliar germ band is re-organised as the teloblasts differentiate. At that point, before the teloblasts begin to proliferate body segments, segmental compartments for the maxillules, maxillae, and first thoracomeres appear all at once on the germ band. Thus, the initiation of all of the duplosegments of the first field and node one in these peracarids are under a different, non-teloblastic control from that of the characteristic teloblastic control of the more posterior fields and nodes. Furthermore, this control is independent of whether the teloblasts are in front of or behind the blastopore, or even if there are teloblasts at all (as in amphipods.)

A similar control to that seen in Crustacea is evident in Cheliceriformes (Table 3; Fig. 11), only in this case the possible gap mutation and forward shift is a synapomorphy for the entire subphylum. Cheliceriforms are characterised by an apparent lack of events in node one. The prosoma extends from the first field into the middle of the second field. It is duplomere 9 that is either the site where the gonopores are located, as in chelicerates *sensu stricto*, or where the abdomen begins, as in fossil and extant pycnogonids and the fossils *Chasmataspis* and *Sanctacaris*. It is possible that node one was completely deleted by a gap mutation in the ancestry of cheliceriforms, consequently producing an apparent shift forward of events out of node two into d_9. Circumstantial support for such a gap mutation in the trunk region of

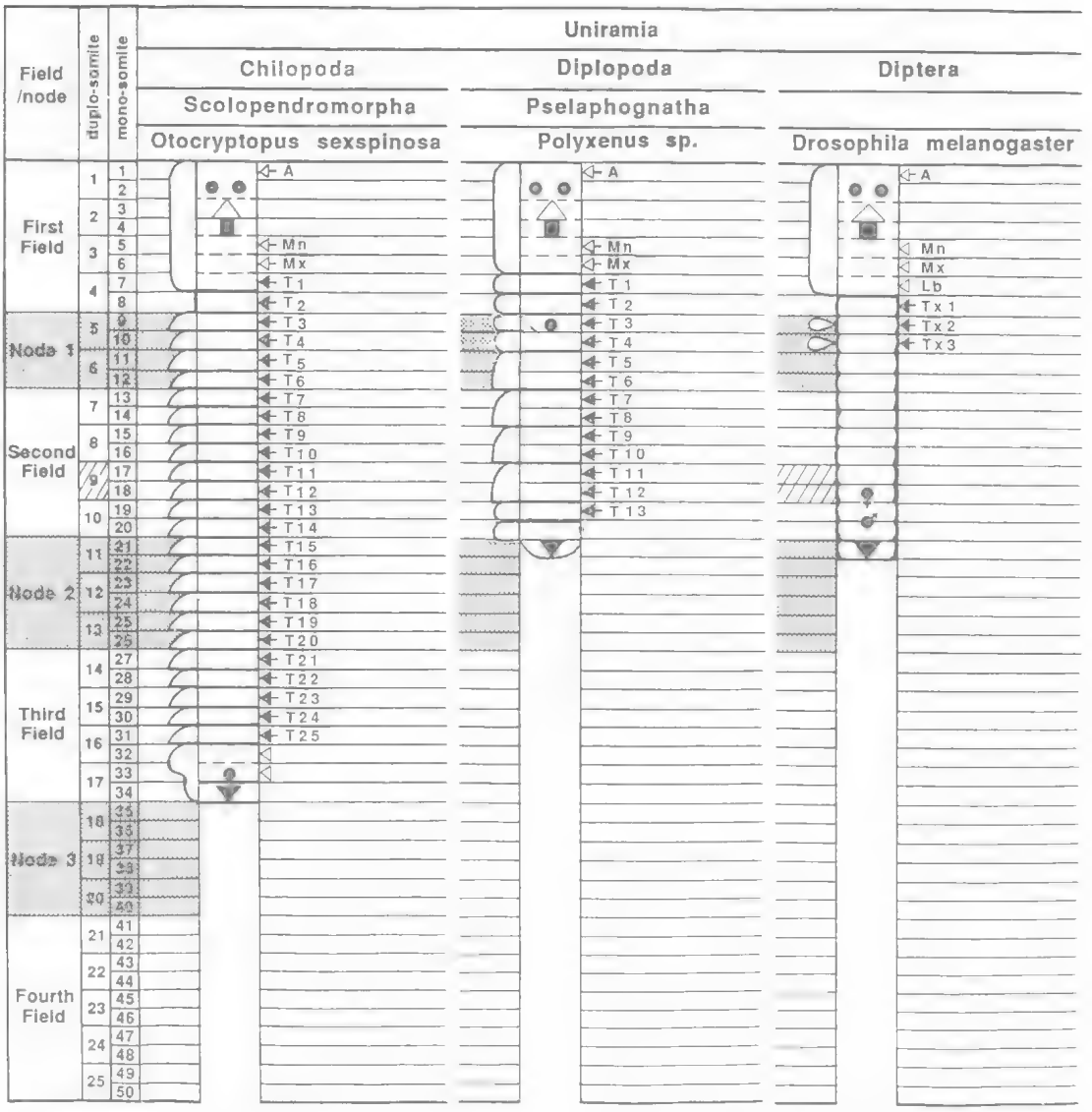

FIG. 10. Diagrammatic representations to illustrate some APT features of living uniramian body plans, with APT numeration to the left. Symbols as in Fig. 9.

cheliceriforms might be sought in the cephalic region of these animals. Cheliceriforms are characterised by loss of the deutocerebral region of the brain, and we are tempted to suggest that the apomorphies of brain structure and tagmatisation of this group of arthropods are related to some mutation(s) in the regulatory control of development that altered the patterns of 'normal' pattern expression by means of gaps in segment development. More typical pattern formation in cheliceriforms seems to prevail in the region posterior to d_9.

In addition to the above animals, various problematic fossil arthropods from the Burgess Shale and other localities appear to conform to APT (Table 4). The patterns among these fossils, compared to those in Tables 1, 2, and 3, lack information on the location of gonopores. In addition some confusion in interpretation arises related to shortcomings in the preservation of these fossils. An example of this is seen with the Cambrian arthropod *Sidneyia*. This animal has traditionally been interpreted as having a single segment head (Bruton, 1981; Gould,1989). *Sid-*

TABLE 1. Segmental patterning in Uniramia with reference to fields and nodes.

Taxa	F^1	N^1	F^2	N^2	F^3	N^3	F^4
Geophilomorpha	hd	hd	+	+	+	+	t a,gp
Scolopendromorpha	"	"	+	+	t a,gp	–	–
Scutigeromorpha	"	begin tr	+	gp,a	–	–	–
Lithobiomorpha	"	"	+	" "	–	–	–
Polydesmoidea	"	gp	+	+	+	+	t a
Ascospermomorpha	"	"	+	+	+	+	"
Juliformia	"	"	+	+	+	+	"
Limacomorpha	"	"	+	+	+	+	"
Colobognatha	"	"	+	gpods	+	+	t a
Oniscomorpha	"	"	+	t a	–	–	–
Pselaphognatha	"	"	t a		–	–	–
Symphyla	"	"	+	t a	–	–	–
Pauropoda	"	"	t a	–	–	–	–
Arthropleura *	"	?gp	+	+	+	t a	–
Insecta	"	tx/abd	t gp	a –	–	–	–
Apterygota	"	"	"	"	–	–	–

a = anus, gp = gonopores, f = female, m = male, ? = unknown but predicted location, t = structure at terminus of region, d_n = duplomere, X/Y = transition, + = segments present but otherwise undistinguished, – = portion of or whole region deleted, hd = head, tr = trunk, tx = thorax, abd = abdomen, * = extinct.

TABLE 2. Segmental patterning in Crustacea with reference to fields and nodes.

Taxa	F^1	N^1	F^2	N^2	F^3	N^3	F^4
Nectiopoda	hd	hd/tr	+	fgp	+	mgp	t a
Tesnusocaris *	"	"	+	?gp	+	?gp	t a
Malacostraca	"	hd/tx	+	gp	+	t a	
Copepoda	"	"	+	gp	d_{16}a		–
Mystacocarida	"	"	$d_9$gp	+	d_{16}a		–
Skara *	"	"	?$d_9$gp	+	t a	–	–
Ostracoda	"	"	+	fgp	d_{16}mgp,a	–	–
Branchiura	"	"	$d_9$gp,a	–	–	–	–
Ascothoracida	"	fgp, "	+	mgp	d_{16}a	–	–
Thoracica	"	" "	+	",a	–	–	–
Lepidocaris *	"	"	+	+	?d_{16}gp	+	t a
Anostraca$_1$	"	"	+	+	"	+	t a
Anostraca$_2$	"	"	+	+	",a		
Notostraca	"	"	+	+	"	+	t a
Conchostraca	"	"	+	+	"	+	t a
Cladocera	"	"	+	gp,a	–	–	–
Leptostraca	"	"	+	gp	+	t abd	a
Canadaspis *	"	"	+	?gp	+	"	"
Cephalocarida	"	"	+	gp	+	+	t a

Abbreviations as in Table 1.

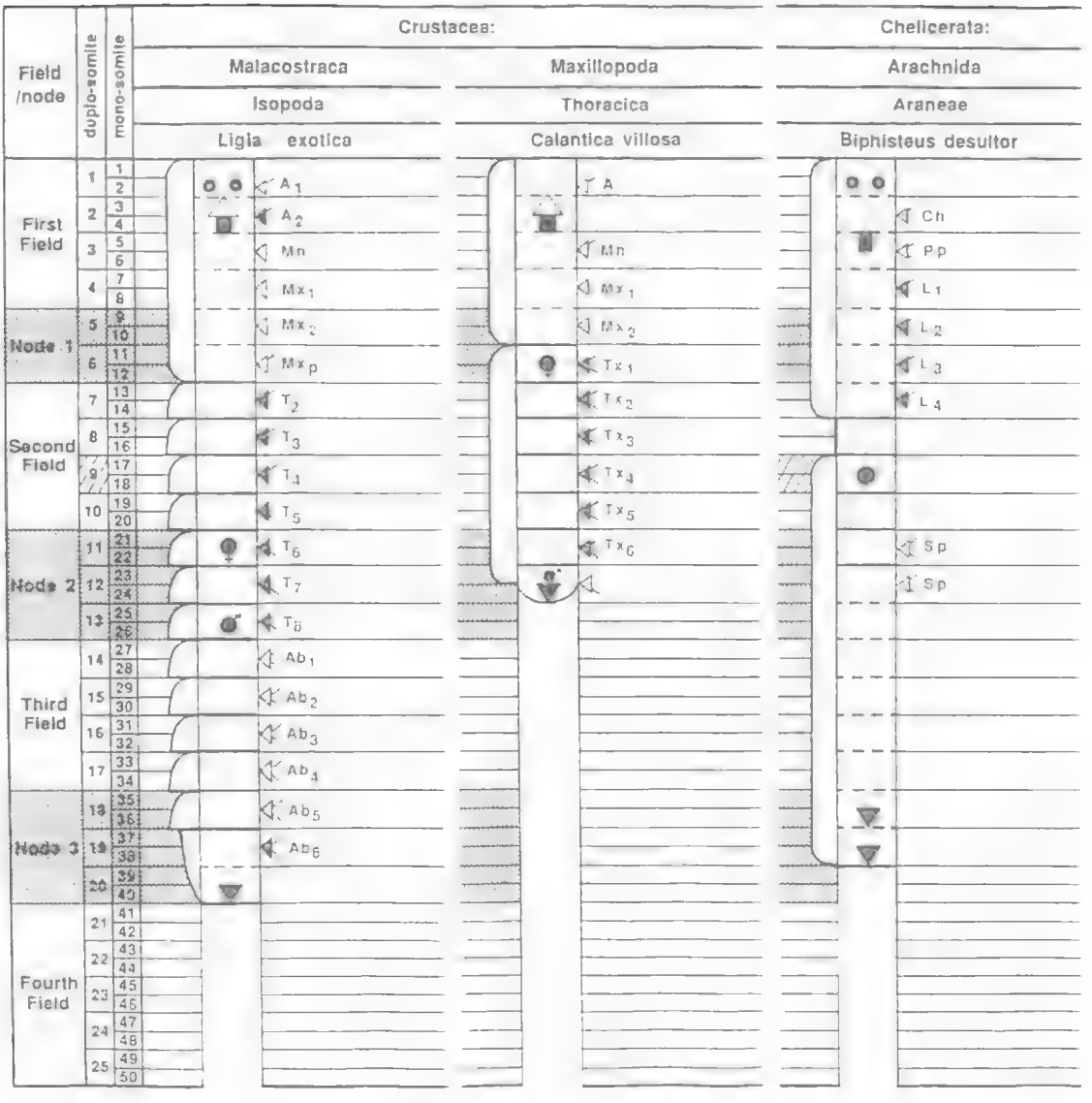

FIG. 11. Diagrammatic representations to illustrate some APT features of some advanced crustaceans and chelicerate body plans, with APT numeration to the left. Symbols as in Fig. 9.

neyia, however, has a rather subtle distinction of limbs that sets off a prosoma of four pairs of uniramous limbs posterior to the mouth from an opisthosoma with five sets of biramous limbs. This transition occurs in node one; the opisthosoma extends through the second field; and a short abdomen (or postabdomen) occupies node two. Under the traditional interpretation, *Sidneyia* is not an APT animal; under our interpretation it clearly is.

While most of the known problematic arthropod genera do display APT motifs in some way, several fossils remain enigmatic. Given the current state of our knowledge about them, the following taxa do not appear to have any APT features: *Burgessia*, *Marrella*, *Mimetaster*, and *Vachonisia*. Whether this lack is real or merely due to an inadequacy in our knowledge about incompletely preserved fossils is not known.

DISCUSSION

In the last 150 years, numerous schemes to explain arthropod phylogeny have been put for-

TABLE 3. Segmental patterning in Cheliceriformes with reference to fields and nodes.

Taxa	F^1	N^1	F^2	N^2	F^3	N^3	F^4
Sanctacaris *	pr	pr	pr/op	+	+	a	–
Palaeoisopus *	"	"	$d_9$abd	t a	–	–	
*Palaeopantopus**	"	"	"	a –		–	–
Pycnogonida	"	"	",gp,a	–	–	–	–
Synxiphosura *	"	"	?$d_9$gp	+	t a	–	–
Chasmataspis *	"	"	?$d_9$gp	+	t a	–	–
Limulus	"	"	$d_9$gp	+	a –	–	–
Erypterida *	"	"	?$d_9$gp	+	+	t a	–
Scorpionida	"	"	$d_9$gp	+	+	t a	–
Araneae	"	"	"	+	+	"	–
Solifugae	"	"	"	+	+	a –	–
Opiliones	"	"	"	+	a	–	–
Palpigradi	"	"	"	+	+	a	
Sternarthron *	"	"	?$d_9$gp	t a	–	–	–
Uropygi	"	"	$d_9$gp	+	+	a	–
Ricinulei	"	"	"	+	a	–	
Acarina	"	"	"	t a	–	–	–

pr = prosoma, op = opisthosoma, abbreviations otherwise as in Table 1.

TABLE 4. Segmental patterning in various problematic fossil arthropods with reference to fields and nodes.

Taxa	F^1	N^1	F^2	N^2	F^3	N^3	F^4
Triarthrus	hd	hd/tr	+	+	+	tr/py	t a
Rhenops	"	"	+	+	+	"	t a
Naroia	"	"	+	+	+	a –	–
Olenoides	"	"		tr/py	d_{17}a–	–	–
Agnostus	"	"	t a	–		–	
Yohoia	"	"	+	+	+	a –	–
Waptia	"	"	+	tx/ab	+	a –	
Oxyuropoda	"	begin legs	+	seg. change	+	a –	–
Actaeus	"	begin tr	+	+	d_{15}a	–	–
Alalcomenaeus	"	"	+	+	"	–	–
Habelia	"	"	+	+	"	–	–
Plenocaris	"	hd/tr	+	+	a –	–	–
Leanchoilea	"	"	+	leg change	a –	–	–
Emeraldella	"	"	+	+	+	a –	–
Molaria	"	"	+	t a	–	–	–
Sartrocercus	"	"	+	t a	–	–	–
Sidneyia	"	hd/tr	+	abd.	a –	–	–
Aglaspis	"	"	+	legs end	a –	–	–
Cheloniellon	"	"	+	seg. change	–	–	–

Abbreviations as in Table 1.

ward, but no consensus has been achieved. For example, workers have either focused on development (Anderson, 1973), or morphology (Snodgrass, 1952; Manton, 1977; Gupta, 1979), or fossils (Bergström, 1979, 1980) and have developed explanations for arthropod evolution narrowly derived from those disciplines. The strength of APT is that it combines information from all these fields of study into one coherent canon.

A measure of the effectiveness of a theory is its ability to make predictions. Unlike other theories about arthropod relationships, APT offers a predictive framework that attempts to prognosticate information yet to be derived from future studies. For example, the discovery of a second set of gonopores in nectiopodan remipedes (Ito and Schram, 1988) corroborated APT because the location of the female gonopores in node two was on the segments that APT predicts. Similarly, APT can be tested by seeking gonopores and/or other structural markers on specific nodal segments on the bodies of the fossil taxa, as indicated in the tables.

Another mark of a theory's strength is how well it incorporates and reconciles apparently disparate elements of previous theories. For example, Snodgrass (1938) united the insect/myriapod and crustacean lines as the Mandibulata. Manton (1964, 1977) disagreed with that position, arguing that mandibles were convergently developed in different arthropod groups. Manton's work was seconded by Anderson (1973) who recognised what he felt were fundamentally different patterns of blastomere fates among the three major groups of living arthropods. Various authors (Gupta, 1979) have disagreed with Manton and Anderson.

A preliminary and very tentative phenogram for arthropods based on APT assumptions (Fig. 12) reveals that these old theories can cease their warring — all incorporate elements of 'truth'. The mandibulates, in the sense of Snodgrass, can be recognized as a paraphyletic group near the base of the arthropod lineage. This arrangement accommodates the continuity of blastomere fates of uniramians extending to onychophorans and clitellate annelids. The unique early ontogenetic patterns so effectively outlined by Anderson for crustaceans and cheliceriforms, can now be seen as autapomorphies for those groups. Mandibles appear to be convergently developed, in the sense of Manton (1964), but this can be accommodated within the concept of arthropod monophyly, in the sense of many authors in Gupta (1979). The concepts of Arachnomorpha (Stormer, 1944) and Schizoramia (Hessler and Newman, 1975) also have validity, and the positioning of many Burgess Shale arthropods relatively high in the arthropod genealogy (Briggs and Fortey, 1989) deserves careful consideration.

Figure 12 is not a cladogram but merely represents at best a crude first guess of possible relationships within the arthropods. A character matrix for APT features is being prepared. How this will translate into a specific cladogram for arthropods must await the completion of that work. However, certain broad patterns can be discerned from the above analysis that prompt us to offer (Fig. 12) a phylogram of arthropod types displaying the distribution of major APT characters and other non-APT features. Essentially, the evolution of arthropods can be seen as a progressive series of events from a diplomerous, uniramous animal through to a fully duplomerous, biramous condition. Some uniramians, such as insects and geophilomorph centipedes manifest a secondary monomery, and cheliceriforms (as well as a few crustaceans) manifest a secondary uniramy. Nevertheless, the main thrust of arthropod evolution appears to have been focused on progressive control over duplication cycles (Minelli and Bortoletto, 1987; Jacobs, 1990) such that diplomeres were fused to form duplomeres, and diplo- and duplomeres were genetically controlled as unit fields and nodes. The end point of this evolution was a developmental and functional system that allowed for more effective limb and tagmata specialisations than were possible in less derived articulates such as annelids.

A confirmation of sorts for the above scheme comes from the study of molecular sequence data. Among the most controversial analyses of molecular phylogeny is that of the 18S ribosomal RNA sequencing of Field *et al.* (1988), wherein metazoans were viewed as polyphyletic. A reanalysis of that data, however, by Lake (1990) reveals a broad pattern of metazoan evolution that is more in accord with traditional interpretations of animal history and a branching sequence for arthropods similar with what we suggest here (Fig. 12). In Lake's analysis, the myriapods and insects are sister groups to the biramian arthropods in a transition series leading to a clade that includes annelids and molluscs. Lake feels the paraphyly of the arthropods evident in his scheme is not strongly supported by the nature of the molecular data available, and that much

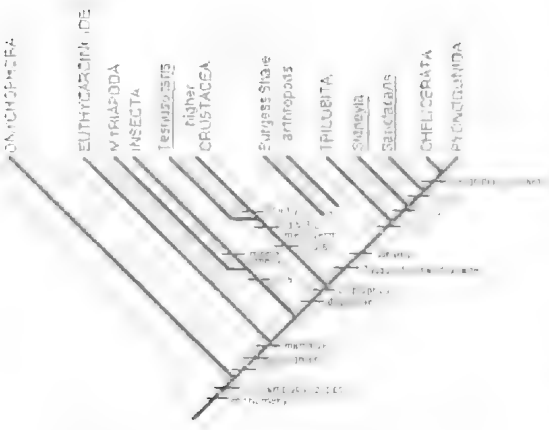

FIG. 12. Phenogram of possible arthropod relationships according to APT portraying the distribution of various APT and traditional characters discussed in the text.

more data are needed from a variety of arthropods before a more definitive answer can be obtained concerning the relationships of protostomes. However, his analysis does seem to support both the idea of the uniramians as an early offshoot of the arthropod lineage, as we advocate here, and the close relationship of crustaceans and cheliceriforms, as suggested by Briggs and Fortey (1989) and by us.

A species is neither completely derived nor completely primitive; each is a mosaic of features suited to the individual functional needs of that species. The challenge of phylogenetic studies is to sort those features and arrive at some judgment of the relative significance of each. We have approached all arthropod characters with an open mind, and willingly entertained the unthinkable by treating even old and long established assumptions as if they were just newly formed hypotheses. Furthermore, we believe much is to be gained by bridging disparate fields of research in an attempt to find common patterns. A certain smugness has formed around the idea that fossils can never really make any substantial contributions toward understanding phylogeny, other than filling in the details of a particular group's history. For example, Wilmer (1990: 76) bluntly stated, 'It actually seems unlikely...that any one author's view of metazoan phylogeny has ever been substantially formed, or substantially altered after formation, by reference to the paleontological record.' In contrast, we feel that fossils can make a great contribution towards understanding animal evolution, as they have in the present case. Furthermore, we caution against too much reliance on the use of exclusive paths to 'truth', e.g. such as those represented by molecular data. All lines of research are productive, but theories are not to be viewed as either entirely true or completely false. They are merely useful for a time in organizing facts and indicating potentially informative lines of research (Wenner and Wells, 1990).

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